HYBRIDIZATION IN THE HAWAIIAN SILVERSWORD COMPLEX

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The Haleakala silversword (Argyroxiphium macrocephalum) Gray is one of Hawai'i's most well-known and publicized endemic plants. Each year it is in fact sought out by hundreds of tourists including many botanists from all parts of the world. However, the 'ahinahina (A. macrocephalum) is only one of six species in the genus Argyroxiphium which includes plants called greenswords as well as those called silverswords. The silversword ordinarily produces a basal rosette of leaves for a number of years before it finally produces a single massive, elongated capitulescence and dies. The floral heads of sword plants are characteristically large and provided with rays. They are found on Hawai'i and Maui, growing in cinder or, as in the case of A. virescens Hbd., in boggy areas like greensword meadow in the upper Hana rain forest on Maui.

Wilkesia, the iliau, is a related bitypic genus which has a growth pattern similar to that of sword plants. It is endemic to dry slopes in and near Waimea Canyon, Kaua'i.

In marked contrast to Argyroxiphium the related Hawaiian endemic genus Dubautia (including Railliardia) is comprised largely of woody, branching shrubs that produce small, rayless heads year after year. However, the genus shows a truly remarkable spectrum of variation from largely herbaceous, low-growing forms like D. scabra (DC.) Keck in dry, pioneer habitats as well as rain forest situations through woody shrubs or small trees like D. linearis (Gaud.) Keck and D. arborea (Gray) Keck in dry sites; and D. raillardioides Hbd. and D. knudsenii Hbd. in wet sites to larger trees like D. reticulata (Sherff) Keck in the vicinity of Pu'u Nianiau. One striking species (D. latifolia [Gray] Keck) from Kaua'i is a large liana with a basal diameter of up to three inches. Altogether there are about 25 species of Dubautia including those called na'ena'e or kupaoa and collectively they are distributed from Kaua'i to Hawai'i.

Field Observations

Dubautia scabra is a widespread species with considerable ecological amplitude and thus comes into contact with several other species of Dubautia. Often the result is spontaneous hybridization as is the case in the upper Hana rain forest. Here the diminutive D. scabra is sympatric with an undescribed large

shrubby Dubautia and numerous hybrids between the two have become established. These hybrids have been given at least four names (Railliardia ternifolia Sherff, R. thyrsiflora Sherff var. cernua Sherff, R. coriacea Sherff, and R. demissifolia Sherff var. dolichophylla St. John). The hybrid plants have an intermediate morphology and pale lemon-yellow flowers, a color that readily distinguishes all known hybrids involving the white-flowered D. scabra.

A second hybrid combination occurring in large numbers also involves D. scabra. In several areas on Hawai'i, including Hawaii Volcanoes National Park, D. ciliolata (DC.) Keck and D. scabra are sympatric. In these instances hybrids between the two have invariably been found. The hybrid morphology is intermediate between the shrubby D. ciliolata and the subherbaceous D. scabra and again the flower color is pale lemon-yellow. These plants have been referred to as D. ciliolata var. laxiflora (DC.) Keck.

A third instance of hybridization involving D. scabra occurs in the vicinity of Pu'u Nianiau, Maui, where one hybrid with the large tree, D. reticulata, has been detected. The hybrid is a very diffuse, spreading plant about 2 m tall. As one would expect it also has pale lemon-yellow flowers.

In the same area, within 50 m of the previous hybrid occur two hybrids between D. scabra and D. plantaginea Gaud., a large shrubby, wide-leaved species. The hybrids are somewhat pendulous and viney with ascending shoot tips and lemon-yellow corollas. They have been given the name Railliardia lonchophylla Sherff var. stipitata (Sherff) Sherff and I suspect that plants of this hybrid combination also occur elsewhere and have been ascribed other names.

Only one hybrid Dubautia combination has been documented from O'ahu. Two individuals of the combination D. sherffiana Fosb. x D. plantaginea have been detected in widely separated locations in the Wai'anae Mts. Both parents are shrubs with orange-yellow flowers and as one might expect, the hybrids are not as morphologically distinct as in the previous cases.

The most spectacular instance of hybridization in this complex occurs in Haleakala on Maui. There, Argyroxiphium macrocephalum, an essentially monocarpic rosette plant with large, radiate heads hybridizes spontaneously with the scrubby, woody Dubautia menziesii (Gray) Keck having small rayless heads that are produced annually. The hybrid is somewhat intermediate in appearance (cf. Kobayashi, 1973). It produces tufts of leaves usually on three or more branches, each of which eventually flowers and dies independently. The hybrid has heads of intermediate size with small yellowish distorted rays.

Cytology

The difference between this and other studies of hybridization involving Hawaiian taxa is that in these instances hybrids can be identified with certainty through an analysis of chromosome pairing during meiosis in floral buds. In each of these cases the parents are differentiated chromosomally and these differences can be positively detected at meiosis. In every hybrid except D. scabra x D. plantaginea the diploid chromosome number is 2n = 27, indicating in these instances that one parent furnished 13 chromosomes and the other parent furnished 14. In all cases the chromosome numbers of the parents are consistent with this argument (cf. Carr, 1978). Although D. plantaginea and D. scabra both have 14 pairs of chromosomes, hybrids between the two can be readily recognized at meiosis by virtue of the fact that their genomes are differentiated by two reciprocal chromosome translocations resulting in the appearance of two chains of 4 chromosomes each (cf. Table 1).

These meiotic perturbations result in the inviability of some of the gametes formed. This depression of fertility can be assessed by the staining reaction of pollen grains in certain dyes like cotton blue. Genetic differentiation between parents can also cause low viability and thus low pollen stainability in hybrid plants. Pollen stainability in the hybrids discussed herein ranges from 6 to 86% (Table 1).

Conclusion

In spite of the spectacular morphological and ecological diversity exhibited by these genera, the occurrence of many intergeneric, intersubgeneric, and interspecific hybrid combinations under field conditions attests to the fact that they form a thoroughly natural, genetically cohesive group that has in all probability resulted from rapid evolutionary differentiation of a single colonizing progenitor. Collectively, these plants constitute what may be considered an unparalleled example of adaptive radiation and as such are exceedingly interesting to students of evolutionary phenomena.

LITERATURE CITED

Carr, G. D. 1978. Chromosome numbers of Hawaiian flowering plants and the significance of cytology in selected taxa. Amer. J. Bot. 65: 236-242.

Kobayashi, H. K. 1973. Putative generic hybrids of Haleakala's silversword and kupaoa (Argyroxiphium sandwicense x Dubautia menziesii) Compositae. Pac. Sci. 27: 207-208.

TABLE 1. *Dubautia* and *Argyroxiphium* spontaneous hybrids.

Combination	Number Examined/Seen	Pollen Stainability %	Diploid (2n) Chromosome Number	Meiotic Configuration	Location
D. scabra x *D.* n. sp.	5/many	57	27	$12_{II} + Ch_3$	Maui
D. scabra x *D. ciliolata*	12/many	76	27	$12_{II} + Ch_3$	Hawai'i
D. scabra x *D. reticulata*	1/1	86	27	$12_{II} + Ch_3$	Maui
D. scabra x *D. plantaginea*	1/2	35	28	$10_{II} + 2\ Ch_4$	Maui
D. plantaginea x *D. sherffiana*	2/2	41	27	$10_{II} + Ch_4 + Ch_3$	O'ahu
A. macrocephalum x *D. menziesii*	2/14	6	27	$9_{II} + 3\ Ch_3$	Maui